INTRASPECIFIC VARIATION, DIVERSITY, REVISED SYSTEMATICS AND TYPE OF THE DEVONIAN STROMATOPOROID, *AMPHIPORA*

by COLIN W. STEARN

ABSTRACT. Understanding of the morphological variation and defining characters of the abundant and ubiquitous dendroid stromatoporoid genus *Amphipora* Schulz has been hindered by the loss of the holotype specimen of the type species, *A. ramosa* (Phillips). In the absence of a type, the boundaries of the genus *Amphipora* could only be defined vaguely, yet 12 genera of *Amphipora*-like fossils have been named to constitute the family Amphiporidae Rukhin, and about 175 species of these genera have been described. Assemblages of amphiporids in a single bed show a wide range of variation but are considered to be the remains of a monospecific stand because a comparable range of variation can be demonstrated along the length of single stems. Some highly variable characters have been used to distinguish genera and species. In particular, the expression of the axial canal, nature and presence of peripheral membranes, thickness of skeletal elements, and density of the skeletal network are shown to be of dubious value as criteria for characterizing genera or species.

A neotype for *Amphipora ramosa* is selected from collections made from the Chercombe Bridge Limestone at the Broadridge Wood Quarry, Newton Abbot, Devon, and revised diagnoses of the species and genus are formulated. The presence of distinct pillars in the neotype and all examined specimens from Devon shows that the four genera whose distinctiveness from *Amphipora* was based on the presence of this character, should be regarded as junior synonyms. Four other genera are also placed in synonymy with *Amphipora*. The amphiporid animal is reconstructed as a small, cylindrical, branching, calcified sponge in which the dermal membranes covering the vestibules were locally calcified to form the peripheral membranes and vesicles.

'A VAST amount of work remains to be done with respect to the Devonshire organic remains; but I rejoice to know that the task has been placed in the hands of Mr. Phillips who is not only well qualified but ready to overcome every difficulty, and it cannot be long before we are supplied with the fullest and most satisfactory information.' (Lonsdale 1840, p. 729)

Much of the synthetic work on diversity trends in the history of life rests on databases dependant on taxonomic decisions. Until now these large databases have been refined to the generic level but progress towards compilation of species diversity is progressing. The numbers of species and genera recognized in fossil groups commonly depends on the taxonomic philosophies of a few specialists. For the last generation, taxonomic work was driven by the conviction that evolution was expressed in the fossil record as gradual morphological change through time. The refinement of biostratigraphical zonation was a goal that led palaeontologists to recognize smaller and smaller morphological differences as new taxa without clear statements of variability in morphology. The plethora of new taxa generated by this work is illustrated by a survey of the genus *Amphipora* and its relatives. This paper documents the variation in a population of specimens of the genus, suggests that most of the genera distinguished from *Amphipora* by characters shared by specimens in a neotype suite are synonyms, and that the 173 species of these genera that have been described do not reflect the real specific diversity of this taxon.

Fossils of *Amphipora* are strewn through Devonian limestones and dolomites like blankets of broken twigs. In these rocks they are the most abundant and geographically widespread of all
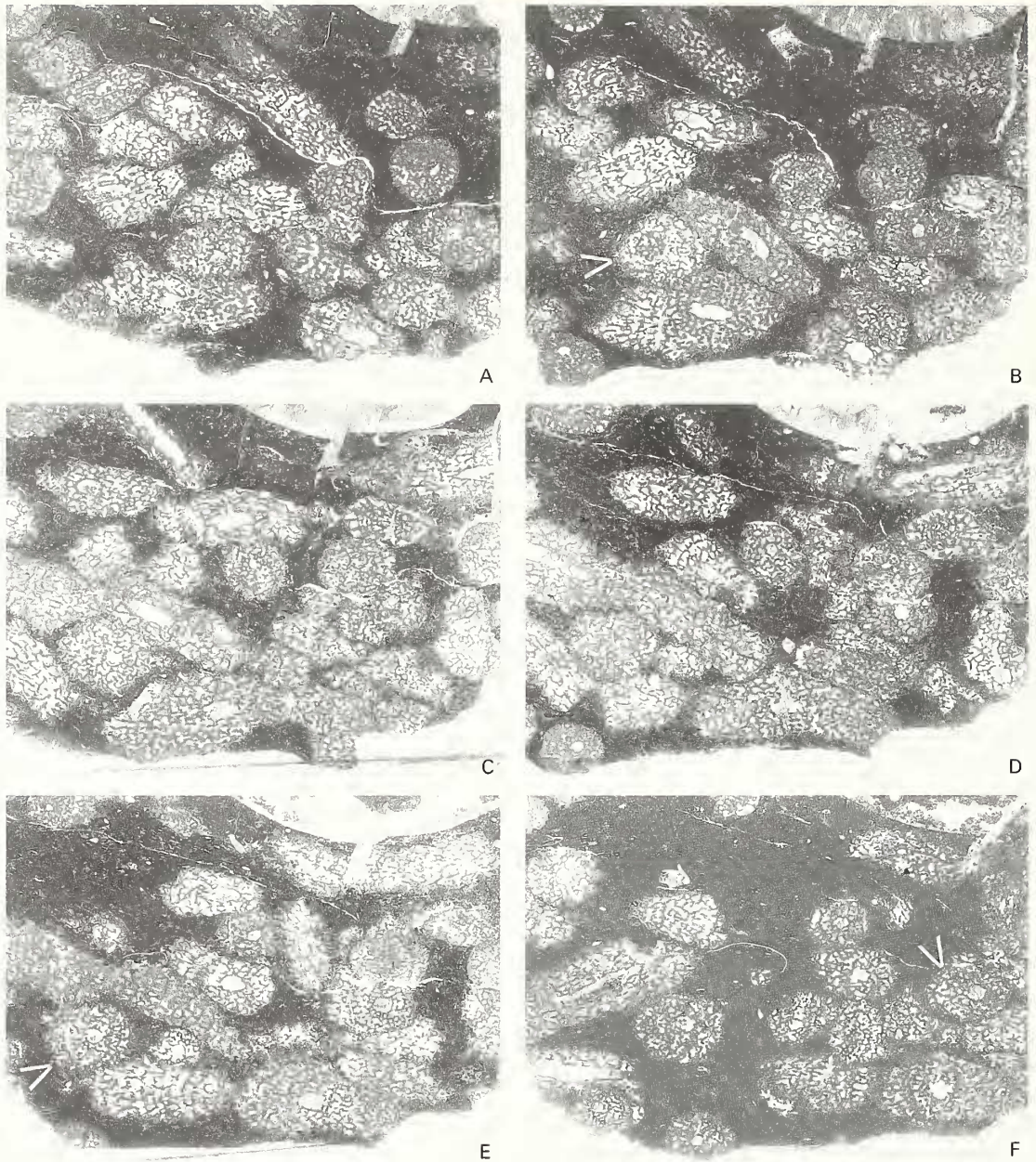
TEXT-FIG. 1. *Amphipora ramosa* (Phillips, 1841); neotype and neotype suite, six serial thin sections from PO 308. The neotype stem is indicated by the V in figures B and E, Broadridge Wood Quarry, Devon. Interval of the sections measured from the first one in parentheses. A, section A1; B, section A2 (1·8 mm); C, section A3 (3·3 mm); D, section A4 (5·1 mm); E, section A5 (6·7 mm); F, section A6 (8·2 mm); see Text-figure 5 for significance of the V. Note the variation in the expression of the axial canal and the pillars in longitudinal and oblique sections. Up/down orientation unknown; all ×2·45.
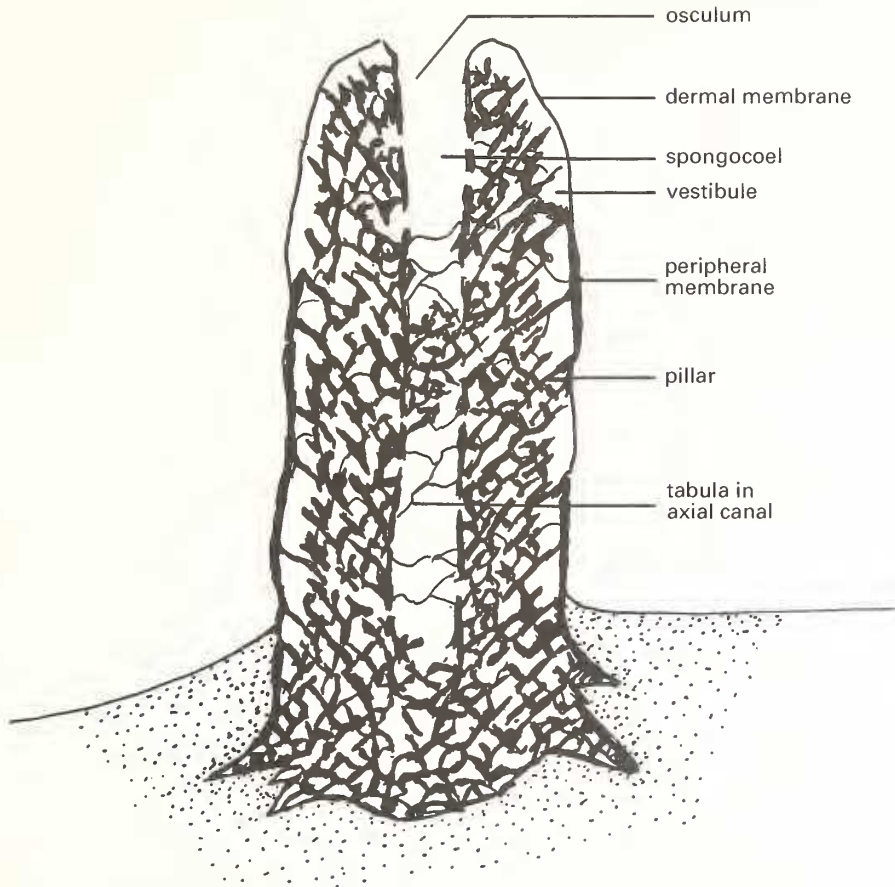
TEXT-FIG. 2. Reconstruction of *Amphipora ramosa* (Phillips, 1841) as a small sponge rooted in the substrate. The reconstruction of the base is speculative.

macrofossils. The 'twigs' are rarely found in isolation; usually they crowd the bed. Despite their abundance and ubiquity (Text-fig. 1), palaeontologists know little about how these organisms lived, how they should be classified, how the genus should be defined or divided into species. Some of this confusion results from the loss of the type specimens of the type species, *Amphipora ramosa* (Phillips).

Typical amphiporid stems are rods a few millimetres in diameter and are composed of skeletal elements of fibrous calcite defining an irregular network of hard tissue in which concentric elements are obscure, and radial elements are hard to distinguish. The voids, or labyrinthine canals between the elements, open on the periphery in apertures of irregular shape or are covered there by a thin hard tissue membrane held off the surface by delicate processes. The peripheral membrane may be present on only some of the stems or only on some parts of individual stems. A prominent axial canal crossed by dissepiments may or may not be present. Text-figure 2 is a reconstruction of the animal growing from the Devonian sea floor; this is discussed in detail at the end of this paper. Stems more than a few tens of millimetres long are rare but some are as long as 50 mm. Amphiporids occur in rocks of Ludlow age; the earliest *Amphipora* may be as old as Emsian, but the genus is particularly abundant in mid and late Devonian strata. The youngest recorded species of *Amphipora* are found in beds near the base of the Famennian Stage in the Czech Republic and

Russian Urals (Friáková *et al.* 1985). However, the discovery of amphiporids in Strunian (latest Famennian) rocks in western Germany has been noted in the informal literature (Weber 1996, *Fossil Cnidaria and Porifera Newsletter*, **25**(1), 9).

All writers on this genus have commented on the great variability of specimens found preserved together in death assemblages. The most obvious of qualitative differences between stems in an assemblage is in the presence or absence of peripheral membranes and axial canals. Nicholson (1886, p. 110) speculated that the membranes could have been abraded off some specimens or they could be reproductive structures that were present only at certain stages or on certain individuals. Similar alternatives have been discussed by most later writers. Despite the erratic occurrence of the axial canal and peripheral membranes in most assemblages, these features have been used as diagnostic characters to differentiate species.

An astonishing 173 species and subspecies of the genera related to *Amphipora* had been described up to 1991 suggesting that it is much easier to describe a new species of these fossils than to do detailed comparisons with known species.

Since the establishment of *Amphipora* by Schulz (1883), the fossil has generally been considered to belong in the class Stromatoporoidea and, with its related genera, in the family Amphiporidae, Rukhin, 1938. Whether the family should be placed in an order of its own or within another order, such as the Clathrodictyida (e.g. Stearn 1980), remains controversial. No consensus exists on the position of the family within the phylogeny of the stromatoporoids but nearly all the features of their skeletons can be found in other stromatoporoid genera and several genera (see below) appear to bridge the morphological gap between the amphiporids and other stromatoporoid orders. The amphiporid genera are considered in this paper to be sufficiently different from those of the Clathrodictyida, to which they were assigned by Stearn (1980), to constitute a separate order of the class Stromatoporoidea; i.e., Rukhin's (1938) family Amphiporidae is recognized as an order (as was initiated by Webby *et al.* 1993). Cockbain (1984) also suggested that the amphiporids should be separated at the highest level from the rest of the stromatoporoids but did not make a formal proposal.

The cylindrical symmetry of the stems implies that the organism was benthic and interacted with its environment in all horizontal directions. The broken stems may branch dichotomously but no rooting structures or growing tips have so far been positively identified. The organisms are commonly assigned a baffling function in the marine environment (as part of the baffler guild of Fagerstrom (1987)), but are only rarely found in the upright position of growth as they should be if sediment accumulated around the stems as they 'baffled' the current flow.

Some of the problems in the interpretation of this genus considered here are as follows.
1. In the absence of the type specimens of the type species of the genus, *Amphipora ramosa* (Phillips), how can the typical form of the genus be determined?
2. Are the many displaced stems of amphiporids found together in most deposits remnants of a monospecific stand, and is the variation found within such assemblages indicative of inter- or intraspecific variation?
3. Did the organism pass through a series of developmental stages as it grew – sequential stages exhibiting changes in features, such as peripheral membranes and axial canals, that have been considered to separate different species or different genera?
4. Type specimens of amphiporids have commonly been designated as an assemblage of stems enclosed together in a rock. Should the holotype be a single stem under the Rules of Zoological Nomenclature?
5. Can the organism be reconstructed and the functions of its hard parts interpreted with confidence?

HISTORICAL SUMMARY

The extensive early literature on the amphiporids has been summarized by Lecompte (1952) and Zukalova (1971) and is not reviewed here. Lecompte (1952) emphasized the uniqueness of the genus among the stromatoporoids and observed that the erratic presence of peripheral membranes could

not be attributed to mechanical abrasion alone. He suggested that the presence of dissepiments in the axial tube and peripheral cavities indicated an astrorhizal function. He described four new species of *Amphipora* and, from his descriptions, based specific differences on: width of stem, presence of the axial canal, thickness of structural elements, differentiation of pillars, presence and size of peripheral membranes, and nature of the dissepiments in the chambers. Zukalova (1971) listed 63 literature references to species of *Amphipora* in her Table 2. She also plotted (Table 3) the ranges of ratios of diameters of axial canals to branch diameters of the species recognized in these papers. She distinguished specimens as *A. ramosa* from the other five species recognized from Moravia by their ratio of over 1:6; that is, the axial canal is proportionally much smaller than in other species.

Cockbain (1984) has discussed problems concerning *Amphipora*. He described the structure as characterized by 'pillars with lateral processes connecting adjacent pillars', lack of laminae, and an outer wall covering the outside of each branch attached to the ends of the pillars and lateral processes. He regarded the fibrous structure as secondary and interpreted the axial canal as not analogous to an astrorhizal canal. The presence of the canal was not considered to be of taxonomic value. Although his specimens included those with a very thin peripheral membrane clearly separated from the inner structure by a wide vesicle (Cockbain 1984, pl. 7), he considered the membrane as homologous to the other structural elements but only half as thick, and the vesicle as a gallery. He illustrated (Cockbain, 1981, fig. 14) a specimen of *A. rudis* in which the axial canal continues up only one of the branches from a division point, and at another branching the canal is absent for a short distance in the newly formed branch, then forms again.

Dong De-Yuan and Wang Chen-Yuan (1982) introduced two new genera of amphiporids whose generic diagnoses imply that the presence or absence of peripheral vesicles and axial canals is diagnostic at the generic level. Dong De-Yuan and Wang Bao-Yu (1984) introduced another genus, *Tianshanostroma*, that was placed in Idiostromatidae but has many characteristics of an amphiporid. They also established a subfamily, Amphiporina, for several amphiporid genera.

In Bogoyavlenskaya and Dan'shina (1984), Bogoyavlenskaya described six new species of her genus *Stellopora* and assigned the genus to the Actinostromatidae. She referred to the extensions from the pillars in this genus as colliculi and ascribed the voids divided by 'tabulae' to an astrorhizal system. Bogoyavlenskaya also described the new amphiporid genus *Novitella* and placed it in the Gerronostromatidae.

Bogoyavlenskaya (1985) affirmed that *Amphipora* is a stromatoporoid and recognized the axial canal as an astrorhizal canal without horizontal branches. She suggested that some species of the amphiporid *Stellopora* originated as high mamelons on the surface of *Actinostroma* that broke off. She reconstructed *Amphipora* as growing in meadows in shallow water but believed, on the basis of the orientation of the axial canal tabulae, that the stems rolled around like logs on the substrate. She postulated that they were coelenterates that obtained the sunlight they required on all sides by their slow rolling. The occurrence of *Amphipora* communities in the Silurian and Devonian of the Urals was discussed in detail. The genera considered in this paper to be amphiporids are placed by Bogoyavlenskaya (1985) in several different orders.

Makarenko (1988) emphasized the unity of the amphiporids and noted that Bogoyavlenskaya's (1985) division of them into different orders did not take into account their distinctive microstructure. He believed the dendroid growth form that also unites the group to be genetically dictated. Much of his paper is a review of the stratigraphical distribution of *Amphipora* species in the west Siberian region.

LOCATION OF THE TYPE SPECIMEN OF *AMPHIPORA RAMOSA*

The first mention in the literature of *Amphipora* is in Lonsdale's (1840) paper on the Limestones of South Devonshire. In a list of fossils (pp. 737–738) he refers to *Favosites*? *ramosa* from near Chudleigh. The note on this entry reads: '*Favosites*? *ramosa* in the collection of specimens from the Eifel presented to the Geological Society by Mr. Willimott, is labelled *Favosites ramosa* (nob.). It
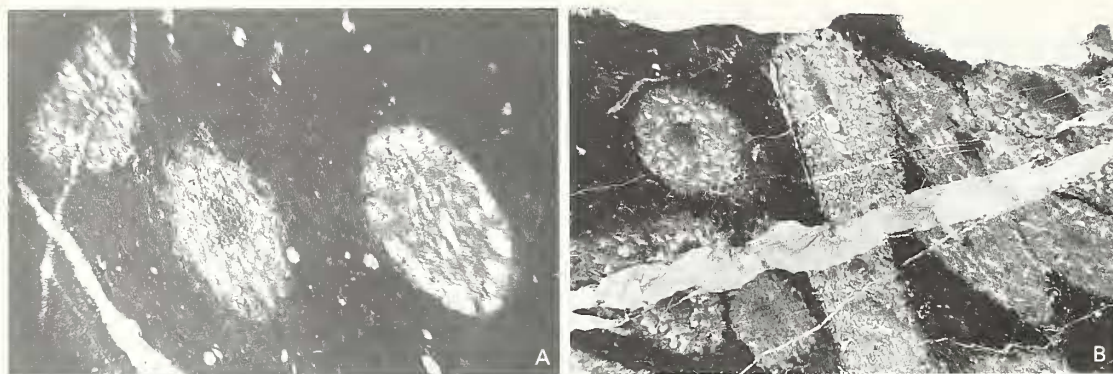
TEXT-FIG. 3 *Amphipora ramosa* (Phillips 1841). A, specimen in the Geological Survey, London (in 1964, now presumably at the British Geological Survey, Keyworth, Nottingham), numbered 52873, labelled as 'possible syntype'; ×9·7. B, specimen (McGill, Redpath Museum RM 20.5340) from top of the Palace quarry, Chudleigh, Devon, showing the poor preservation but general similarity to the Broadridge Wood Quarry specimens; ×4·85.

was obtained originally from M. Brassart of Bonn. The specimen is evidently not a *Favosites* but its state of decomposition and that of several others kindly lent to me by Mr. Murchison, forbid the characters being properly ascertained. The fossil consists of long slender branches perforated down the centre, and presents a carious [sic] structure resembling that of the genus *Scyphia* [a sponge].'

Phillips (1841) described the stems that were later to be named *Amphipora* as *Caunopora ramosa* from Devonian limestones at Chudleigh and Babbacombe in Devon. Schulz (1883), in describing similar fossils from the Eifel district of Germany, established the genus *Amphipora* using Phillips' species as the type.

Unfortunately Phillips' specimen, the holotype of the species, and hence typical of the genus, cannot be found. I have searched for the specimen at The Natural History Museum, the Geological Survey, London (in 1964), and at the University Museum, Oxford. A specimen then at the Geological Survey (and presumably now at Keyworth) marked 'possibly syntype' does not correspond with Phillips' drawing of the type. It is numbered #52873, cut on five of six sides, and labelled 'pres. Geol. Soc. 1911'. It is accompanied by a slide numbered 52873A (Text-fig. 3A). In a letter of July, 1964 H. Dighton Thomas stated that 'It seems highly improbable that it is a syntype'. Some of Phillips' specimens have been located at Oxford University (J. M. Edmonds, pers. comm. June 1964), for instance Phillips' (1841) plate 10, figure 29c (*Caunopora placenta*), plate 10, figure 28a (*Stromatopora concentrica*), plate 8, figure 23 (*Favosites spongites*), but the specimen of *Caunopora ramosa* is not among them. Colin Scrutton (pers. comm. June 1990) recounted a story, that cannot be authenticated, that some of Phillips' material at Oxford was stolen long ago by thieves who thought they had something of value and was then dumped by them in the River Thames when they realized that they had only rocks.

I have examined some specimens (Text-fig. 11A) at the Institut für Paläontologie, Bonn, whose labels suggest they may have been used by Schulz but these do not have the status of types. Most amphiporids are preserved embedded in limestones, but Schulz's specimens from the 'ramosabänke' in the Hillesheim district are preserved weathered out in three-dimensional relief (Schulz 1883, pl. 23, fig. 1) in a light-coloured carbonate that appears to be dolomite. However, the specimens at Bonn cannot be matched exactly with the excellent illustration that accompanies Schulz's paper. Similar exceptionally preserved specimens are in the Nicholson Collection at The Natural History Museum, London, (Nicholson 1886, pl. 9, fig. 1) and must have come from the same bed. Although the outer surfaces of these specimens are preserved in relief, the internal structure of the stems is obscure. Nicholson was the first to use thin sections extensively for the description of stromatoporoids, and his illustrations (Nicholson 1886, pl. 9, figs 1–4; 1892, pl. 29, figs 3–7) of

specimens from Hebborn (Paffrath district, Germany) and South Devon (Teignmouth and Shaldon) became the standards by which *Amphipora ramosa* was known. Benton (1979) recorded that the specimens identified by Nicholson as from Teignmouth are labelled on the slides as from Shaldon, a village on the other (south) side of the estuary of the Teign River. However, the genus is based on a typical species that was originally inadequately described and whose characters cannot be determined accurately in the absence of a type specimen.

DESIGNATION OF A NEOTYPE

Phillips' localities for *Caunopora ramosa* were Chudleigh and Babbacombe. The latter is a suburb of Torquay and Colin Scrutton (pers. comm. 1990) suggested that the specimen was a beach pebble. Early collectors in Devon, including Nicholson, collected many specimens from the beaches, particularly at Teignmouth and Shaldon. Since these specimens were Devonian clasts washed out of Permo-Triassic conglomerates on to Recent beaches, nothing can be deduced about their original stratigraphical position. Beds bearing abundant *Amphipora* are exposed south of Chudleigh and particularly at the top of the Palace Quarry (SX 8682 7871; see Scrutton 1969, 1977). A sample for this study was collected there but the preservation is not good and the specimens are sheared, distorted and the microstructure is obscure (Text-fig. 3B). Much better material was collected from two levels in the Chercombe Bridge Limestone at the Broadridge Wood Quarry on the banks of the Lemon River near Newton Abbot (SX 839 711; Scrutton and Goodger 1987). Most of the observations made here on *Amphipora* are based on the Newton Abbot specimens.

Amphipora was clearly an opportunistic species, spreading rapidly in low diversity communities to the exclusion of other taxa when conditions were appropriate. It would seem ecologically unlikely that several species of a single genus (and therefore having similar environmental requirements) would grow in a meadow–like stand in Devonian seas; such stands in modern marine environments are generally almost monospecific and must have resembled modern marine grass communities. However, to establish that the variability seen in different individuals in a random cross section of an aggregate could be present within a single species, this variability must be shown to exist within an individual stem. To investigate this, the stems in the samples were serially sectioned by grinding down a block and recording the polished surface at 0·5 mm intervals by photographs or camera lucida drawings. Because the structure for a short distance into the polished surface can be observed albeit vaguely, such polished surfaces do not give a clear picture of the structure in a single plane. This process also destroyed the specimen. A clearer picture of the structure was obtained by making successive thin sections which could be retained as evidence of the changes along the length of the stem. These were made by cementing the polished block to glass with an ultraviolet-setting adhesive, cutting the block as close to the glass as possible with an Ingram cutoff saw, smoothing the surface by light grinding and recementing the block to make the next section. The closeness of sections is limited by the thickness of the saw blade to about 1·5 mm, but single stems could normally be traced through many cuts by this method (Text-figs 1, 4–5). Variations in the structure were recorded in photographs and drawings made by tracing the structure on enlarged negative prints. In all, 19 thin sections were cut from the suite of the neotype. Random sections of material from Devon, the Eifel and Ardennes, western Canada, and other localities were also examined. Variations in the structure at various stages of growth are best examined in sections that cut the long axis of the stem.

Neotypes. Three blocks of limestone rich in *Amphipora ramosa* were collected from the Chercombe Bridge Limestone at the Broadridge Wood Quarry (SX 839 711). A map of the quarry, its geology, and a stratigraphical section have been published by Scrutton and Goodger (1987). The *Amphipora*-rich beds are of mid Givetian age according to Scutton (1977). Each block was cut into many fragments to make the thin sections. Specimens in the first block collected about 15 m above the quarry base on the path at the east side of the quarry face are designated as the neotype suite and an individual stem, represented by six serial thin sections (PO 308.A1–A6) and the remnant
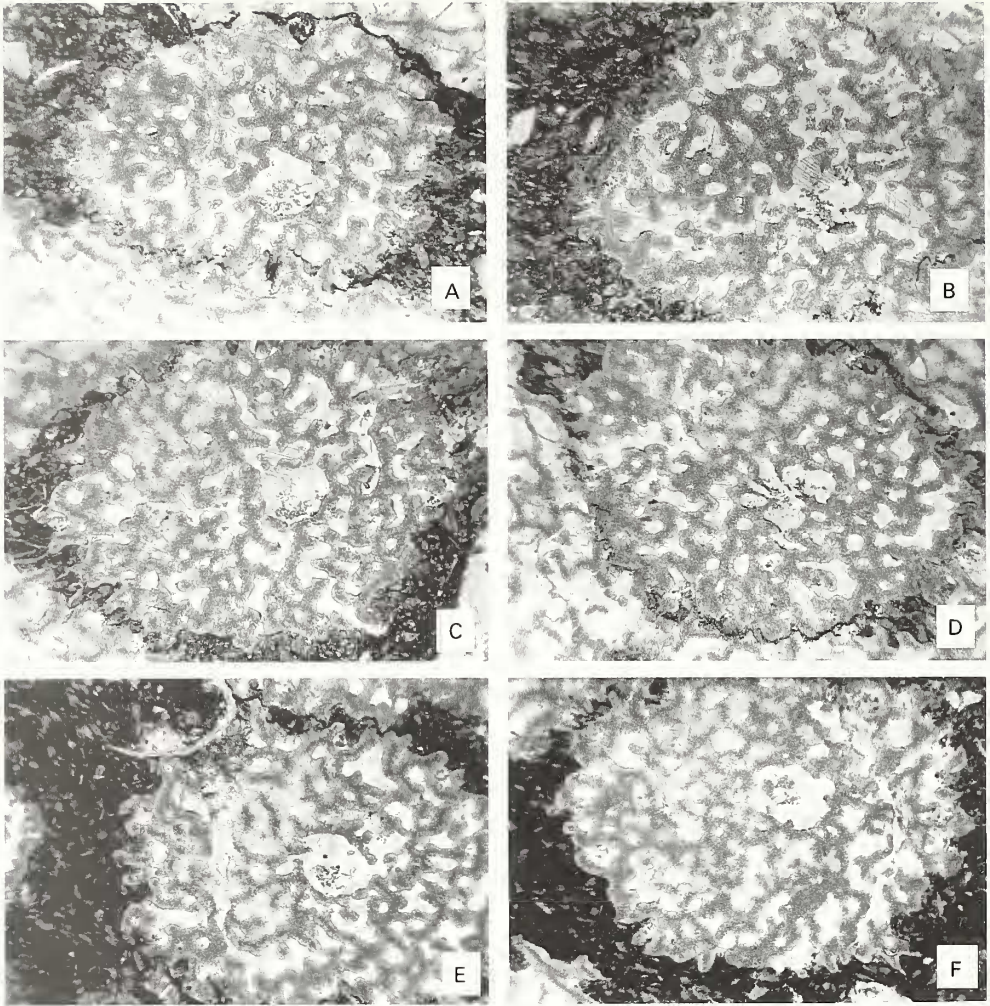
TEXT-FIG. 4 *Amphipora ramosa* (Phillips, 1841); neotype stem PO 308.A1 to PO 308.A6, six serial thin sections taken from the slides in Text-figure 1 at the intervals recorded in that caption. Position of the stem shown by the V in Text-Figure 1B and 1E. Note the variation along the stem of the axial canal, the proportion of labyrinthine canals and closed spaces, and the thickness of the skeletal elements; × 10.

block from which they were cut, is designated as the neotype and deposited in The Natural History Museum, London, type collection, under number PO 308. The bed from which the neotype sample was taken is about 21 m above the base of section C of Scrutton and Goodger (1987) and is estimated to be about 129 m above the base of the Chercombe Bridge Limestone (Colin Scrutton, pers. comm. 1996). A second block from the other side of the quarry about 1 m stratigraphically below the neotype suite is designated a neoparatype (PO 309) and the sections from it are numbered PO 309.B1–B5. A third block, loose at the base of the quarry, collected by Stephen Kershaw, is micritic and the specimens in it show well-developed peripheral vesicles. This suite of specimens is designated as another neoparatype PO 310 and the thin sections from it are numbered PO 310.C1–4.

Although one stem is designated as the neotype (Text-fig. 4), the assumption is made in this description that all the stems in the neotype asemblage belong to the same species. Serial sections of several stems of the suite (Text-figs 4–7) are illustrated to show that the variation within

individuals is comparable to that in individual stems of the suite and justifies this assumption. The use of aggregates of stems to illustrate species of *Amphipora* by authors such as Lecompte (1952) and Zukalova (1971) shows that they also tacitly made this assumption. An additional assumption made in the description is that the stems grew vertically so that the axis defines the vertical dimension.

SYSTEMATIC PALAEONTOLOGY

Class STROMATOPOROIDEA Nicholson and Murie, 1879
Order AMPHIPORIDA Ruhkin, 1938
Family AMPHIPORIDAE Rukhin, 1938

Remarks. Rukhin (1938) included the genera *Amphipora* Schulz, *Idiostroma* Winchell, *Haraamphipora* Rukhin, and *Zelopora* Penecke in the new family. *Idiostroma* resembles the other amphiporids only in growth form and axial canal; its well defined tripartite laminae place it clearly in the Stromatoporellida. *Haraamphipora* is discussed below. *Zelopora* does not occur in Penecke's work and may be a misprint of *Zeapora* Penecke (Berhard Hubmann, pers. comm. 1996). The nature of this fossil is under investigation by Hubmann. It has been considered a bryozoan (Bassler, 1953, p. G236).

Genus AMPHIPORA Schulz, 1883

[= *Amphipora* Schulz, 1883, p. 245; *Haraamphipora* Rukhin, 1938, p. 93; *Paramphipora* Yavorsky, 1955, p. 154; *Vicinustachyodes* Yavorsky, 1961, p. 56; *Stellopora* Bogoyavlenskaya, 1972, p. 27; *Taeniostroma* Dong and Wang, 1982, p. 29; *Columndictyon* Dong and Wang, 1982, p. 29; *Tianshanostroma* Dong and Wang, 1984, p. 269; *Qinghaipora* Dong, 1991, p. 75].

Revised Diagnosis. Skeleton dendroid, branching dichotomously, with axial canal locally absent, locally with well–defined wall, locally poorly defined, opening by pores into the interskeletal network of voids and irregular canals. Skeletal network formed by pillars radiating upward and outward obliquely from axis and short elements extending from, and joining them to form an irregular structure that may in cross section define open or closed spaces. Peripheral vesicles sporadically developed in most species, bounded by an imperforate calcareous membrane supported beyond the skeletal network by extensions of the skeletal elements. Microstructure compact, fibrous.

Remarks. The major change in this diagnosis from those now widely used is in recognition of the importance of the pillars radiating upward and outward from the axial canal and of the intrageneric variability of the skeletal structures. Most of the early illustrations of *A. ramosa* (Phillips 1841; Schulz 1883) and the description of M'Coy (1885) indicate the presence of pillars diverging upward and outward. The impression that such pillars are not characteristic of *Amphipora* may have been given by Nicholson's illustration of specimens from Devon (1892, pl. 29, figs 1–7) and from Hebborn (1886, pl. 9, figs 2, 4) that show these pillars vaguely, if at all. However, oblique sections from the same slide as Plate 9, figure 2 (Nicholson's No. 399) clearly show the radiating pillars (Text-fig. 11B). The pillars have been made a diagnostic generic character of the genera *Stellopora* Bogoyavlenskaya, *Columndictyon* Dong and Wang, *Tianshanostroma* Dong and Wang and *Qinghaipora* Dong. The evidence presented here shows that these four genera cannot be distinguished from *Amphipora* on this basis. Other genera distiguished from *Amphipora* on criteria of questionable validity, because they are expressed to various degrees in most suites of amphiporids, include: *Vicinustachyodes* Yavorsky, *Paramphipora* Yavorsky, *Haraamphipora* Rukhin, *Taeniostroma* Dong and Wang. All eight genera are considered here to be junior synonyms of *Amphipora* Schulz.

Rukhin (1938) established the genus *Haraamphipora* (type species: *H. pachyroides* Rukhin, 1938) on the basis of its thickened skeletal elements, a highly variable feature within individual stems. This genus has generally been considered to be a synonym of *Amphipora* (Yavorsky 1962; Flügel and

Flügel–Kahler 1968; Zukalova 1971). Structural elements of typical *Amphipora ramosa* have an opaque axis coated on both sides by fibrous calcite (Stearn 1977, pl. 3, fig. 3). Yavorsky (1955) distinguished a new genus *Paramphipora* (type species: *P. mirabilis* Yavorsky, 1955) from *Amphipora* on the basis of the absence of this dark axis. In the first and subsequent publications he named 34 new species of this new genus. In all, Russian and Chinese palaeontologists have named 42 species assigned to this genus. Stearn (1966, 1980), Klovan (1966), Flügel and Flügel–Kahler (1968) and Zukalova (1971) have doubted the validity of *Paramphipora* because minor diagenetic changes can obscure the microstructure of *Amphipora*, yielding specimens that would be placed in *Paramphipora*.

In 1961 Yavorsky proposed another amphiporid genus, *Vicinustachyodes* (type species: *V. mirabilis* Yavorsky, 1961). He (Yavorsky 1967) later changed the spelling of the name to *Vicinostachyodes*. The genus is distinguished from other amphiporids by the absence of an axial canal (a feature absent in many specimens of *A. ramosa*). Only Yavorsky (1961, 1967) has named species of this genus and it does not appear in the summary of Soviet genera by Bogoyavlenskaya and Khromych (1985).

Stellopora Bogoyavlenskaya, 1972 (type species *Amphipora intexta* Yavorsky, 1957) was established for fossils similar to *Amphipora* that in axial section show long pillars radiating upward and outward to the peripheral membranes. Webby *et al.* (1994) commented on the original (Bogoyavlenskaya 1971) naming of this taxa as *Columnoporella* (preoccupied). Although this genus has been used for about 20 species (mostly by Bogoyavlenskaya) its validity is doubtful as evidence presented below shows that the diagnostic pillars are prominent features of *Amphipora ramosa*.

Dong and Wang (1982) proposed two new genera of amphiporids: *Taeniostroma* (type species: *T. yunnanense* Dong and Wang, 1982) and *Columndictyon* (type species: *C. regulare* Dong and Wang, 1982). For the former of these, distinguishing features were listed as irregular skeletal elements without opaque axes, an axial canal, and lack of peripheral vesicles. All these features are known in what is considered here as typical *Amphipora ramosa*. *Columndictyon* is said to be distinguished by the differentiation of the pillars and slightly arched discontinuous laminae, the lack of axial canals and peripheral vesicles (although figures in Dong and Wang's plate 18 suggest that both may be present in the type species). Comparison with the similar genus *Stellopora* is not made in this description (Webby *et al.* 1994). Dong and Wang (1982) also described the new genus *Eostachyodes* (type species: *E. compacta* Dong and Wang, 1982). This genus is not clearly an amphiporid and is classified with the Stachyoditidae by Dong (1988).

Dong and Wang (1984) proposed the amphiporid genus *Tianshanostroma* (type species: *T. xinjiangense* Dong and Wang, 1984). Webby *et al.* (1994) commented on the similarity of this genus to *Stellopora* Bogoyavlenskaya. Like this genus, it has upward and outward radiating pillars best seen in oblique sections. *Qinghaipora* Dong, 1991 (type species: *Q. gracilenta* Dong, 1991) is based on poorly preserved specimens from the Devonian of China. Webby *et al.* (1994) suggested that this genus also could be a synonym of *Stellopora* Bogoyavlenskaya.

The genus *Vacuustroma* Hung and Mistiaen, 1997 (type species: *V. michelini* Hung and Mistiaen, 1997; from *Amphipora* sp. Mistiaen 1988, p. 188), was established for amphiporids with coarsely porous or vacuolate microstructure.

Other genera of Amphiporidae. The first of the amphiporid genera proposed by Bogoyavlenskaya (1965) was *Clathrodictyella* (type species: *Amphipora turkestanica* Lessovaya, 1962). The structure in cross section is much like that of *Amphipora* but in axial section the structural elements appear as upwardly convex cysts vaguely defining laminae that bend down at the periphery. The genus appears to be confined to the Upper Silurian but may extend into the lowermost Devonian. *Euryamphipora* Klovan, 1966, (type species: *E. platyformis* Klovan, 1966) is the only amphiporid with a laminar growth form. The skeleton is a plate of interlaced irregular skeletal elements bordered above and below by marginal vesicles. Cockbain (1984) reconstructed the skeleton as a vertical plate and synonymized the genus with *Amphipora*. Mistiaen (1985) described Frasnian specimens of the genus from Afghanistan as having grown horizontally.
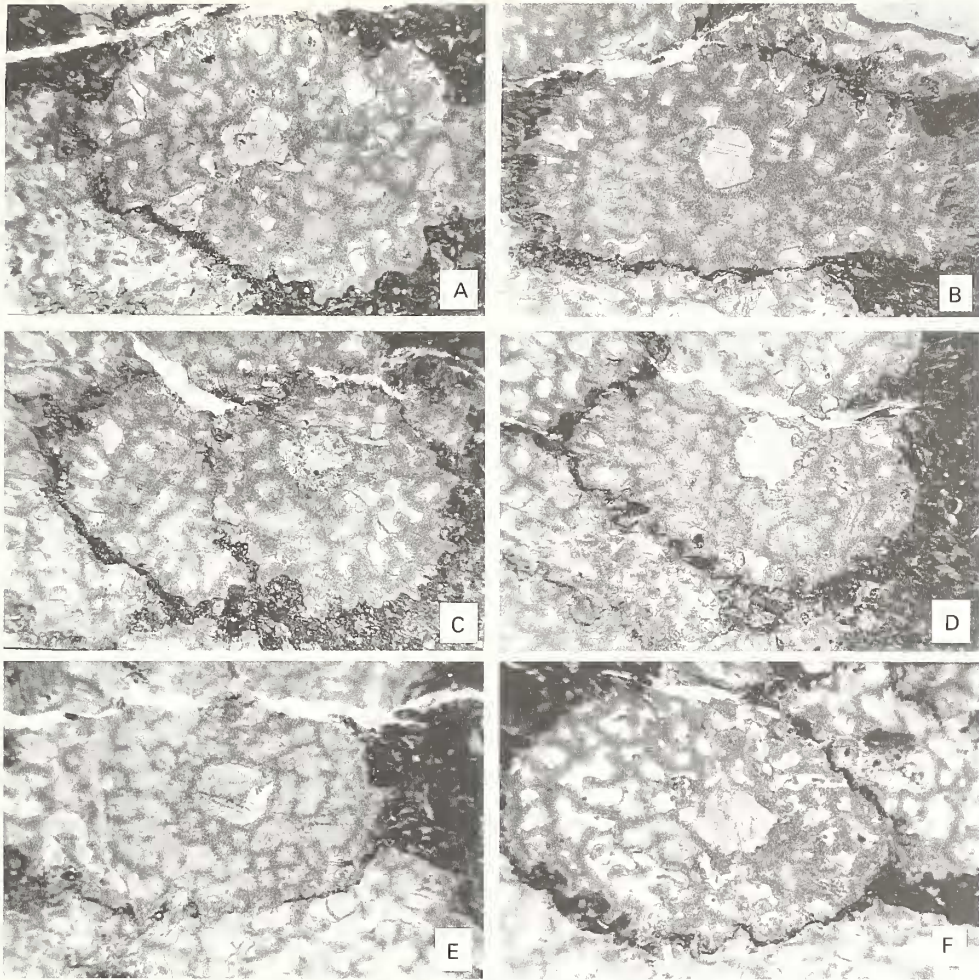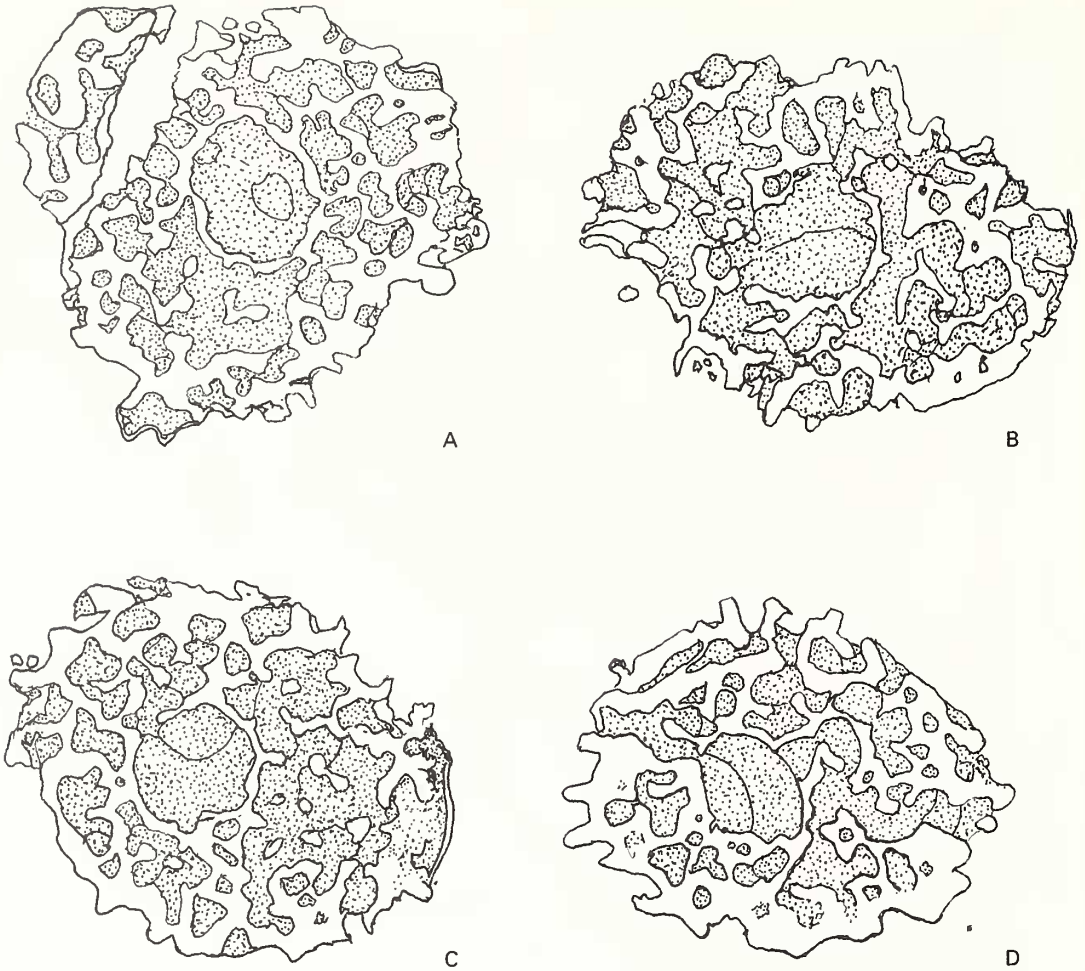
TEXT-FIG. 5. *Amphipora ramosa* (Phillips, 1841); six serial sections from the slides of the neotype suite PO 308.A1 to A6. The location of this stem is shown by the V on Text-figure 1F. Same intervals as for Text-figure 1; × 10.

Bogoyavlenskaya (1984 *in* Bogoyavlenskaya and Dan'shina 1984) erected the amphiporid genus *Novitella* (type species: *Paramphipora tschussovensis* Yavorsky, 1955), although she placed it in the Gerronostromatidae. The cross section is much like that of other amphiporids, with axial canal, peripheral vesicles and irregular structural elements, but oblique sections show gently arched laminae and short pillars confined to interlaminar spaces.

The genus *Eostachyodes* Dong and Wang, 1982 (type species: *E. compacta* Dong and Wang, 1982) resembles *Amphipora* and was described with a group of amphiporids but is probably best classified with the Stachyoditidae, as suggested by Dong (1988).

Two other genera related to *Amphipora* have been described but are unlikely to belong in Amphiporidae. *Clavidictyon* Sugiyama, 1939 (type species: *C. columnare* Sugiyama, 1939), from the Silurian of Japan, appears to be an amphiporid lacking an axial canal in transverse section, but has well defined single layer laminae and short post pillars in peripheral parts of the stems. Examination of the type thin section indicates that the species *C. japonicum*, also named by Sugiyama on this

TEXT-FIG. 6. *Amphipora ramosa* (Phillips, 1841); sketches from tracings of four serial thin sections of a stem from the neotype suite but from a set of sections not illustrated in Text-figure 1, showing a more open structure with larger axial canal. A, section PO 308.A10 (0·0 mm); B, section PO 308.A9 (2·0 mm), also illustrated as Text-figure 7D (mirror image); C section PO 309.A8 (3·4 mm); D. section PO 309.A7 (5·0 mm); Scale bar represents 1 mm.

slide, cannot be differentiated from the typical species. Although placed by Stearn (1980) in the amphiporids, *Clavidictyon* seems now better placed in the Clathrodictyida. *Shirdagopora* Lessovaya, 1987 shows superficial resemblance to the amphiporids but can not be placed neatly in any family at present.

The family Amphiporidae can be considered to be made up of the following five genera:
   *Amphipora* Schulz;
    Clathrodictyella Bogoyavlenskaya: shows convex cysts in axial sections;
    Euryamphipora Klovan: distinguished by plate–like growth;
    Novitella Bogoyavlenskaya: shows discrete laminae and short pillars in axial sections;
    Vacuustroma Hung and Mistiaen: vacuolate structural elements.
Genera that closely resemble amphiporids but are best placed in other higher taxa include:
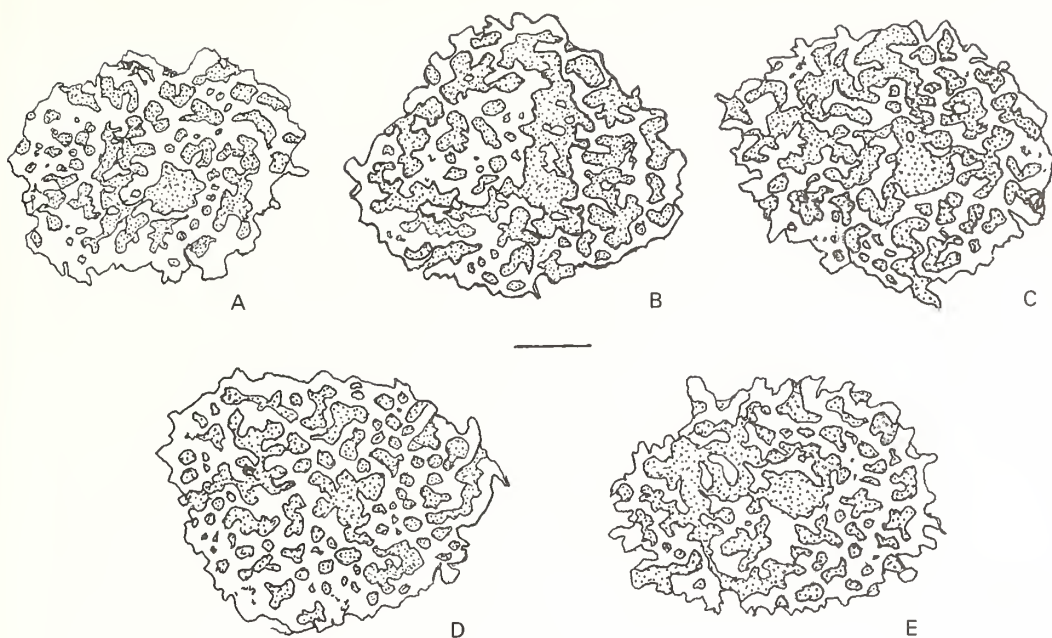
TEXT-FIG. 7. *Amphipora ramosa* (Phillips, 1841); sketches from tracing of serial thin sections of the neotype (sections PO 308.A1 to A5). A, from section A1 (0·0 mm); B, from section A2 (1·8 mm); C, from section A3 (3·3 mm); D, from section A4 (5·1 mm); E, from section A5 (6·7 mm). Note that in C most of the internal spaces are continuous. Up/down orientation unknown. Scale bar represents 1 mm.

Clavidictyon Sugiyama: Clathrodictyidae;
Eostachyodes Dong and Wang: Stachyoditidae;
Shirdagopora Lessovaya: *incertae sedis*.

Amphipora ramosa (Phillips, 1841)

Text-figures 1–11

Caunopora ramosa Phillips, 1841, p. 19.

Recently published synonymies of this species include those of Flügel and Flügel–Kahler (1968), Zukalova (1981) and Cockbain (1984). Preparation of a complete synonymy would require the comparison of the nearly 175 described species of amphiporids with the neotype and is beyond the scope of this paper.

Revised diagnosis. Amphipora with average diameter of about 3·5 mm; wide zone of structural elements; where developed, a narrow axial canal (0·05–1 mm) and zone of peripheral vesicles; well developed pillars at 45°; variable in thickness of skeletal elements, density of their network, and development of axial canal and peripheral membranes.

Description

Skeleton. Stems cylindrical, in all known specimens broken into segments up to 50 mm long, commonly branching dichotomously, rarely showing evidence of lateral budding; without obvious root but some specimens seem to have irregular outgrowths or overgrowths that could be a root system (Text-fig. 8A). Growing tip rarely observed in random sections, rounded with wide, open axial canal into which sediment may penetrate (Text-fig. 9B). Stem diameters show a wide range of values. The mean of 38 measurements of the neotype suite is 3·26 mm (range: 2·0–5·0 mm; standard deviation 0·63 mm).
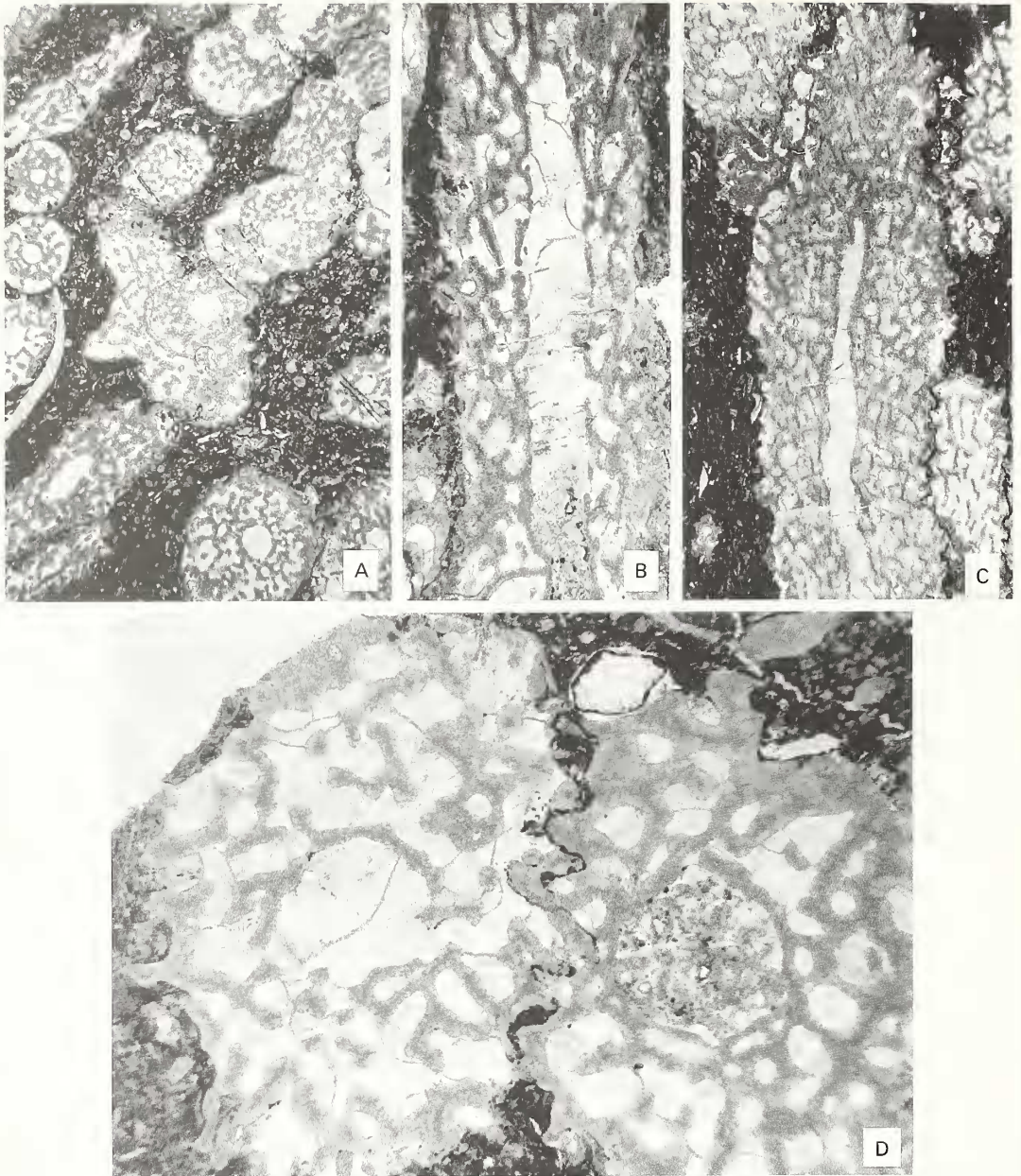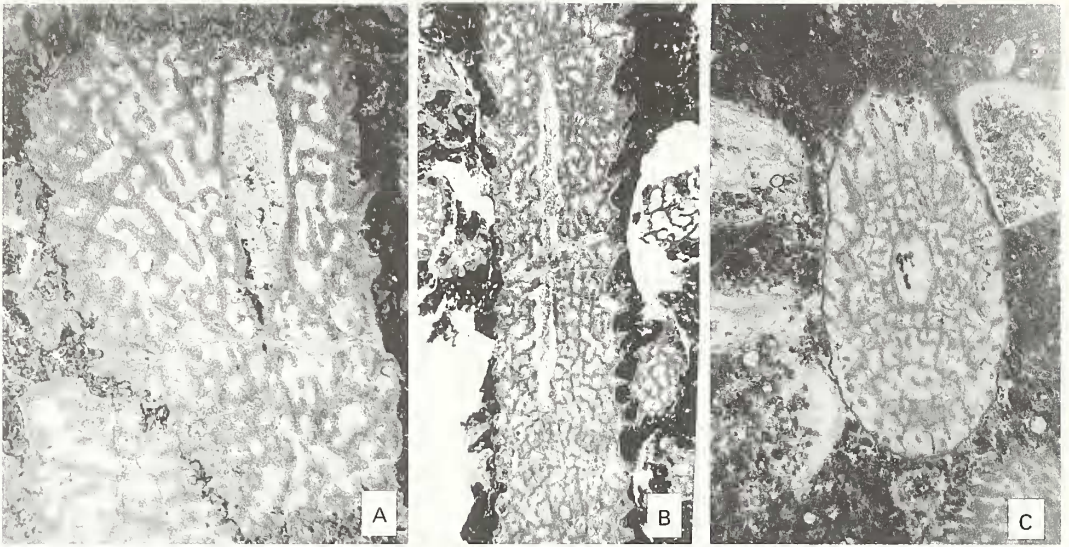
TEXT-FIG. 8. A, *Amphipora ramosa* (Philips 1841)?; specimen from core (McGill Redpath Museum RM 20·5341), Swan Hills field, north central Alberta at 8901 ft [10-34-63-11W5th mer]. Note the outgrowth on the central stem that could be a root structure and the great variation in axial canals and peripheral membranes in a single slide; × 5. B–D, *Amphipora ramosa* (Phillips, 1841). B, neoparatype PO 309.B3; axial section, showing wide axial canal with many pores, well-developed pillars, and a poorly developed peripheral membrane on the middle left; × 10. C, neotype suite PO 308.A15; axial section, showing discontinuous membrane, well developed in the upper right and largely absent below on this side, well-developed pillars holding the membrane, and tabulae crossing the axial canal; × 5. D, section PO 308.A9; cross sections from the neotype suite, showing fibrous microstructure, post-and-bridge construction, dissepiments and tabulae; internal spaces largely open in the stem on the left and closed on that on the right; × 20.
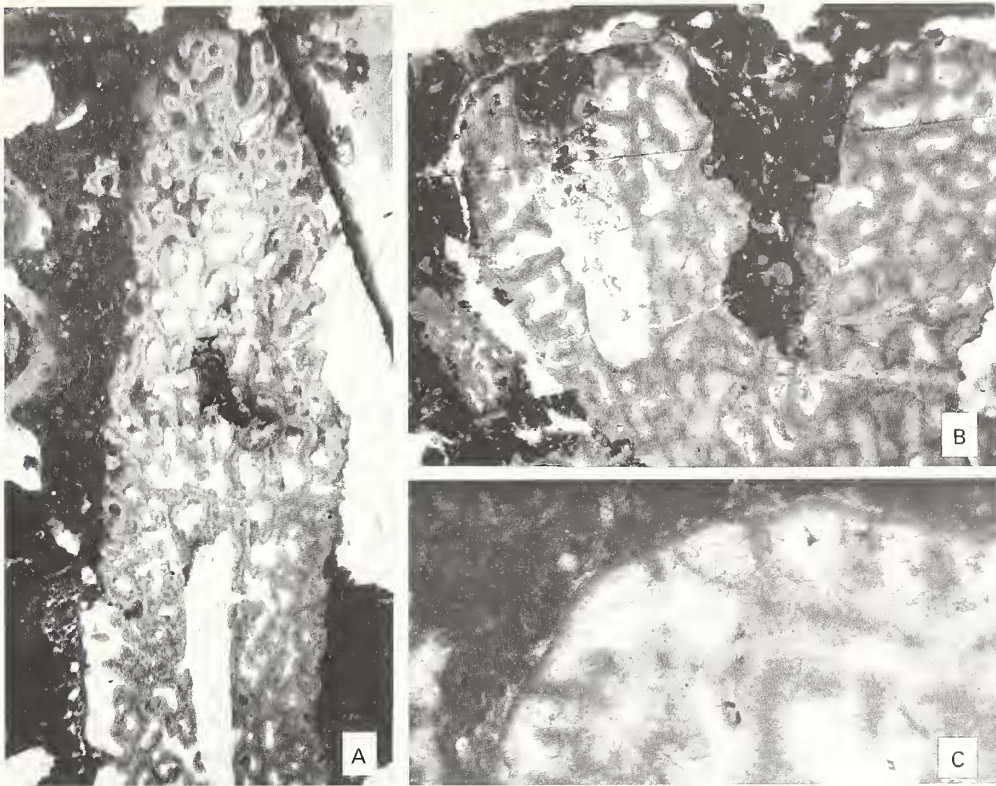
TEXT-FIG. 9. *Amphipora ramosa* (Phillips, 1841); Broadridge Wood Quarry. A, neoparatype PO 310.C6; axial section, showing infilling of upper part by fine sediment and well-developed peripheral vesicle at lower left ending upward without breakage; × 8. B, neotype suite section PO 308.A11; axial section, showing branching and a distal tip with open axial canal infiltrated by sediment; × 10. C, section PO 308.A19; very thin peripheral membrane and narrow vesicle, cross section of neotype suite stem, also showing the fibrous microstructure; × 25.

Axial canal. The canal is present in most stems, obscure or completely unrecognizable in a few, generally bounded by a distinct skeletal wall (Text-fig. 8D), crossed by thin, curved dissepiments of irregular form. Mean of 31 diameters of neotype suite 0·73 mm (range: 0·47–1·0 mm; standard deviation: 0·17 mm). Mean of ratio of axial canal diameter to stem diameter in these specimens 0·22 (range: 0·12–0·39). Canal opening laterally through pores into irregular interskeletal spaces or into canals extending towards the periphery (Text-fig. 8B, D). Highly irregular and locally incomplete tabulae cross the axial canal (Text-fig. 8B–D).

Skeletal network. Skeletal elements commonly 100 to 200 μm thick, possibly diagenetically thickened, highly variable in form and thickness, locally forming an open network in which skeleton forms a small proportion of the stem (Text-figs 4B, 8D), locally almost filling the stem leaving small round interskeletal cavities (Text-figs 4A, 5A–B). In cross section the skeleton appears to be constituted either of isolated pillar-like elements commonly connected by bridges (Text-fig. 8D) or, particularly near the axial canal, of a continuous network inclosing small circular spaces (or canals). Locally the structural elements define and border irregular, tortuous canal systems radiating toward the periphery (Text-figs 4B–C, 8D). Interskeletal spaces crossed by very thin, curved dissepiments (Text-fig. 8D). In axial section the skeleton is cut as an irregular network through which thin pillars curve upward and outward at *c.* 45° from the axial canal to the periphery, commonly supporting the peripheral membranes (if present) at their distal ends (Text-figs 8B–C, 10C). The skeletal network in axial section shows no evidence of parabolic growth lines or structural elements parallel to the growth surface. In oblique sections the pillars are prominent and form an irregular grid with subhorizontal structural elements (Text-fig. 10A, C).

TEXT-FIG. 10. *Amphipora ramosa* (Phillips, 1841). A, section PO 308.A12; oblique section showing the pillars and bridging skeletal elements, neotype suite; ×10. B, section PO 308.A14; axial section, neotype suite, showing complete lack of peripheral vesicles; ×5. C, section PO 308.A15; oblique section showing well-developed thin continuous peripheral membrane, axial canal, and pillars, neotype suite; ×5.

Microstructure. Pillars that are cut across show radial fibrosity (Text-figs 8D, 9C) around a more opaque centre. Linear elements have an opaque axis bordered on either side by a layer of fibrous calcite (Stearn 1977, pl. 3, fig. 3).

Peripheral structures. Three conditions exist at the periphery and more than one condition may exist in a single stem.
1. The structural elements may protrude into the matrix in the absence of a peripheral membrane and the matrix may penetrate a short distance between these elements (Text-figs 1, 4–5). Only rarely does it penetrate deeply into the interskeletal spaces (Text-fig. 9A) that are filled typically with cavity-filling spar. The penetration may be stopped by a transverse skeletal element of normal thickness, a thin dissepiment, or a throat that is too small for the clasts of the grainstone matrix to enter.
2. The structural network is bordered by a membrane of the same thickness as the structural elements (c. 100 μm) that incloses vertically elongate spaces as peripheral membranes. These spaces may be impersistent along the length of the stems (Text-figs 8C, 9A).
3. A delicate, continuous peripheral membrane (< 50 μm) surrounds a spar-filled cavity crossed only by the pillar structures that support it and by dissepiments. The width of the inclosed vesicle ranges from one-half to a small fraction of the radius of the stem (Text-figs 8A, 9C, 10C).

The peripheral membranes, where well preserved, appear to be imperforate. Where one is absent (condition 1) canal systems may extend from the axial canal to the matrix by tortuous courses.

Diagnostic features. Within the wide range of variation shown by the neotype suite, what features have potential to be used in distinguishing the species from other species of the genus or differentiating other genera within the family Amphiporidae? The following features that show wide variation within the individual stems or suite here considered to be remnants of a monospecific stand, are certainly not species specific:
1. presence, absence, or form of peripheral membranes;
2. presence, absence, or distinctness of the axial canal;

3. density of the structural network and thickness of the elements;
4. form and abundance of dissepiments.
Features that have potential for separating *A. ramosa* from other species are:
1. the relative constancy of the diameter of the stems;
2. the relatively small diameter of the axial canal and its proportion of the total diameter of the stem;
3. the pillars spreading upward and outward from the axial canal.

Comparison with Phillips' and Schulz's material. Why should the suite of specimens described above be accepted as representative of Phillips' species *Caunopora ramosa*? They are not strictly topotypes because Phillips' only bedrock locality was apparently the ridge of the Chercombe Bridge Limestone south of Chudleigh about 5 km north of the Broadridge Wood Quarry. Evidence that the neotype is representative of Phillips's material can be found in comparisons with nineteenth century descriptions and illustrations of these fossils from Devon (there are no twentieth century studies), specimens from Devon in museums, and topotype material collected from Chudleigh.
1. Phillips' illustrations (1841, pl. 8, fig. 22a–c) show a stem with relatively small axial canal. The axial section clearly shows the pillars curving upward and outward from the axial canal. Although the diameter of the stems is not given, measurements of the figure suggest that it is about 3·5 mm, (cf. average of 3·26 mm in neotype suite).
2. Schulz's oblique sections clearly show the prominent pillars typical of the neotype in stems 3–4 mm in diameter, peripheral membranes, and a relatively wide structural zone.
3. Specimens from near the type locality, presumably south of Chudleigh, although poorly preserved, show a similar form and range of variation as those in the neotype suite (Text-fig. 3B).
4. M'Coy's (1855, p. 67) description of specimens from Teignmouth mentioned the 'plates ... radiating obliquely upwards and outwards from the large central channel to the surface.'.
5. Nicholson's (1892, pl. 29, figs 1–7) illustrations of specimens from Teignmouth show similar, widely varying, proportions to the neotype but do not faithfully represent the pillars. His (1892, p. 225) remarks on the extraordinary variability of Devon *A. ramosa* and his opinion that 'It is most probable that these different forms are really different conditions of a single type ...' are strongly supported in this study.

The great variability of the Devon specimens places the validity of the almost 175 species of amphiporids in doubt; their validity must be reassessed. Even a casual survey of these species indicates that the range of variation seen in the neotype specimen and neotype suite includes that of many species described from the Middle and Upper Devonian of various parts the world.

FUNCTIONAL MORPHOLOGY

As mentioned in the introduction, the symmetry and branching of *Amphipora* show that it must have stood upright on the sea floor in underwater 'meadows', but no trace of a root has been described. Possibly, like the aulacerids described by Cameron and Copper (1994), they reinforced their bases by biocementation of the surrounding carbonate substrate. The irregular outgrowths on some specimens encountered in random sections may be a spreading root system or another individual wrapped around a stem (Text-fig. 8A). Their symmetry and branching preclude an existence rolling on the bottom as suggested by Bogoyavlenskaya (1985), nor is there any evidence connecting their occurrence with domical stromatoporoids with high mamelons that broke off.

The distal growing tip has been identified in only two stems of the neotype suite (Text-fig. 9B). In random sections the tortuous course of the stems makes following the axial canal throughout its length in a section almost impossible. In the section illustrated here the tip is rounded, the canal is open at the end and coarse sediment has penetrated into the opening. This configuration and the canals that are evident in some sections radiating from the axial canal directly through the structure suggest that this is a modified astrorhizal system, as suggested by Lecompte (1952). The axial canal has also been shown to open at the end of branches in other cylindrical stromatoporoids, such as
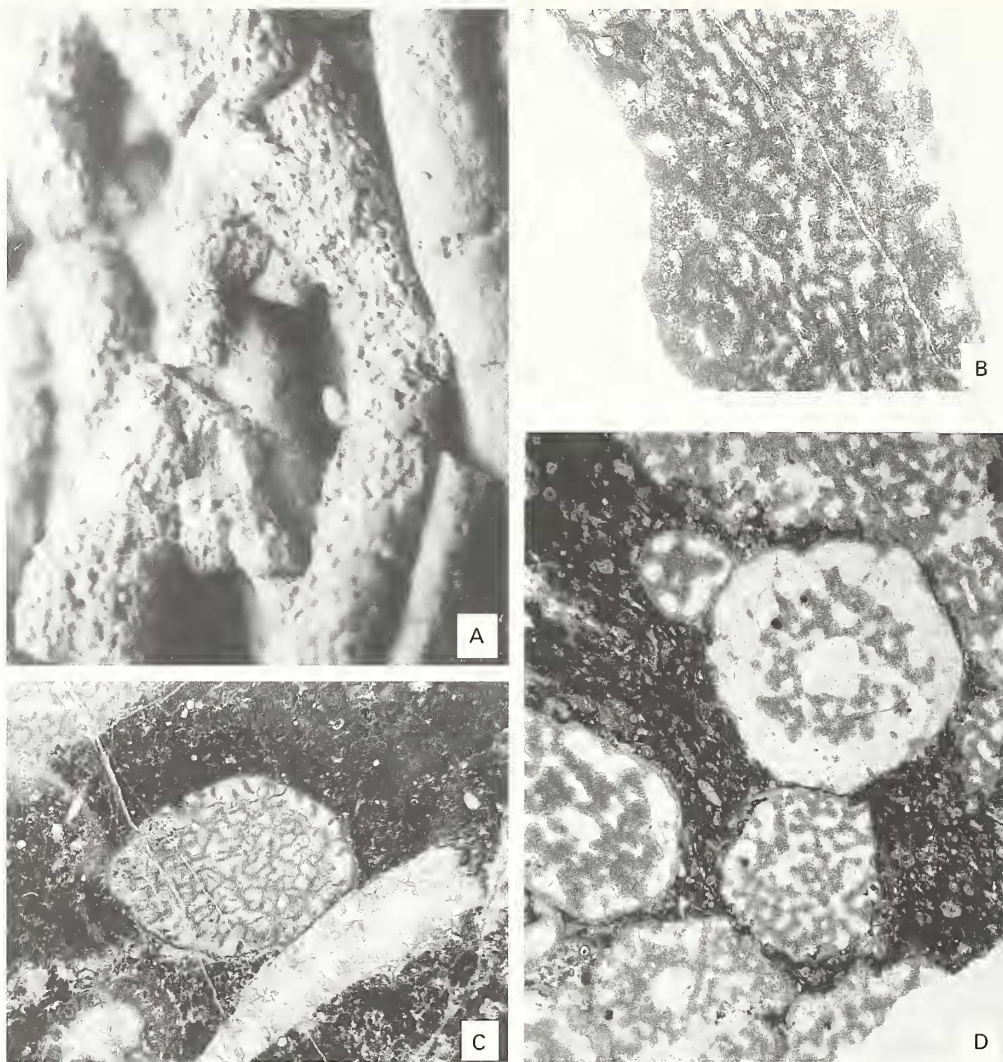
TEXT–FIG. 11. A–C. *Amphipora ramosa* (Phillips, 1841). A, exterior surfaces of a specimen from Schulz's 'ramosabänke' showing some stems with the smooth outer surface of the peripheral membrane, others with open canals; Bonn University, Paläontologische Institut; ×3. B, previously unillustrated tangential section from Nicholson's No. 399 specimen from Hebborn, Germany(Natural History Museum P6071), showing the pillars not clearly illustrated by Nicholson (1886); ×10. C, section PO 308.A15; slightly oblique section, neotype suite, showing thin vesicles and no trace of an axial canal; ×5. D, *Amphipora ramosa* (Phillips, 1841)?; cross sections, Swan Hills field Alberta (as Text-fig. 8A, McGill Redpath Museum RM 20.5341), showing extreme variation in size of stems, complexity of structure, development of the axial canal, and width of the peripheral membranes in a small area; ×10.

Stachyodes. However, unlike the internal structure of other cylindrical stromatoporoids, such as *Stachyodes*, that of *Amphipora* does not preserve successive surfaces parabolic in axial section and parallel to the rounded growing tip.

In nearly all the samples examined, regardless of whether the peripheral membranes are intact, the open space in amphiporids is filled with calcite spar, generally a coarse cavity–filling spar.

Not only are the interstructural spaces (?galleries) filled with spar, the axial canal is also, except at the open end. Since both interior spaces are commonly crossed by dissepiments, I conclude that, like the lower parts of domical stromatoporoids or tabulate corals, they were closed off by the organism as it grew and were empty of organic matter when the organism died. The living tissue was then confined to the upper part of the stem (Stearn and Pickett 1994).

In the specimens studied here, a growth series has not been demonstrated, but variation in the thickness of the structural elements and density of the structure in a single stem is evident (Text-figs 1, 4–5). The thickening of structural elements by overgrowth in the older parts of invertebrate skeletons is well documented in the coralline sponge *Astrosclera* and may also have taken place in *Amphipora*.

Many stems of the neotype suite do not have evident peripheral membranes. In some a membrane clearly separates a narrow vesicle from the matrix, and in many the ends of the structural elements protrude into the matrix. In stems with peripheral membranes in parts of the stem, there is no evidence of breakage at the point where the membrane ends against the structural elements of the stem (Text-figs 8c, 9a). The presence of membranes seems to have some relationship to the matrix in which the stems are embedded. Stems in grainstones rarely have membranes; those in micrites and wackestones commonly have membranes. In the large block collected loose at the bottom of the Broadridge Wood quarry (neoparatype No. PO 310) most of the stems have peripheral membranes. The matrix in these specimens is micritic, finer than that in the neotype, which locally penetrates the interstructural cavities (Text-fig. 9a). Axial sections of this sample show peripheral cavities locally along the length of the stems; these are unbroken where they end against the network of structural elements (Text-fig. 9a). Membranes may be present on one side of a stem and not on the other (Text-figs 8c, 9a). In a sample used for comparison from the Beaverhill Lake Formation (Frasnian) of the Swan Hills area, Alberta, nearly all the stems have peripheral membranes but the width of the cavities they inclose ranges from 0–1000 μm, or from 0–50 per cent. of the radius of the stem (Text-figs 8a, 11d). On the surfaces of Schulz's specimens preserved in three dimensions from the 'ramosabänke' (Text-fig. 11a), the smooth peripheral membrane is present on some parts of the stems and on other parts the rough surface of the ends of the structural elements is evident. In no specimen was an opening seen in this membrane; it appears to have completely sealed the skeleton. From these observations the following conclusions are drawn.

1. The absence of membranes on stems is not everywhere a result of abrasion of the stems, because broken membranes are only rarely found.
2. The development of the membranes is part of the normal growth of *Amphipora*.
3. The membranes did not form only on the base as the organism grew but are sporadically present along some stems.
4. Where present, the membranes sealed off the interior of the skeleton.

Structures possibly analogous to the *Amphipora* membranes have been noted in some other stromatoporoids but their preservation is extremely rare. Nicholson (1886, pp. 59-60) noted the presence of 'a thin apparently structureless calcareous membrane, largely or wholly imperforate' or (p. 110) 'a kind of calcareous pellicle', on several domical and encrusting stromatoporoids. Nicholson (1886, p. 60), Cockbain (1981, pp. 28, 30) and Zukalova (1971, p. 101) reported a thin calcareous membrane on specimens of *Stachyodes*. Structures similar to the peripheral membranes occur in the soft tissue of the coralline sponges *Ceratoporella* and *Stromatospongia* (Willenz and Hartmann 1989). Inhalent water enters a vestibule above the skeleton through microscopic pores in a dermal membrane and passes into the choanocyte chambers within the top of the skeleton. Within the vestibule, water exhaled from the choanocyte chambers is separated from the inhalent water by confinement in a gathering system of tubes analogous to the astrorhizal canals of stromatoporoids. Stearn (1975) has reconstructed domical stromatoporoids with a dermal membrane and vestibule. The calcification of such a membrane as the inhalent surface became non-functional in older or damaged or buried parts of the skeleton would produce a membrane-and-vesicle structure much like that of *Amphipora*. Perhaps such a sealing of the skeleton was required in environments that were rich in fine sediment.

In most deposits the diameter of the stems is relatively constant and strictly axial sections (i.e. those that include the axial canal for much of their length) do not show an increase in width that would be indicative of growth in girth. Such stems are invariably cylindrical. However, some assemblages contain small skeletons of simple internal structure (Text-figs 8A, 11D) that could have been juveniles. In the absence of conical stems, the amphiporid animal is reconstructed as cylindrical throughout its growth (Text-fig. 2) and thin stems are considered to have been unsuccessful and malnourished individuals.

The amphiporid animal can be reconstructed as a small sponge growing in shallow, calm waters periodically swept by storms. The stem was anchored inefficiently by irregular outgrowths at the base or cemented into the substrate. The growing tip had a central opening or osculum that acted as an exhalent pore but extended into a shallow cavity as a spongocoel, blocked below by a tabula. From the spongocoel, collector canals ran irregularly to choanocyte chambers within the structural network. The living tissue was confined to the growing tip; as the soft tissue died, older parts of the skeleton were partitioned off internally by dissepiments and sealed off externally by calcification of the dermal membrane. During growth the exhalent drainage system was at times reorganized so that the walls of the spongocoel broke down and the discreteness of the axial canal was lost. Similar reorganizations of the aquiferous system in living sponges are common and in many stromatoporoids the location of the homologous astrorhizal system was ephemeral. Some of the sponges branched; others remained single. Periodically the *Amphipora* meadows were despoiled by storms that broke the sponges from their bases, fragmented them, and swept them into environments where they did not live. In Devon and western Canada the association of *Amphipora* with grainstones rich in calcispheres suggests that these enigmatic capsules could be related to the propagation of this sponge.

CONCLUSIONS

The large range of variation shown within individual stems of *Amphipora* and suites of specimens preserved together places in doubt the validity of genera separated from the genus and the many species of these genera that have been included in the family Amphiporidae. Description of new taxa in this group should be accompanied by a clear statement of variation along the stem. The illustration of single cross or axial sections is inadequate to establish a new taxon. This study also illustrates that the plethora of generic or specific taxa in the literature may not be a guide to true taxonomic diversity. It suggests that the generic diversity of the family Amphiporidae should be reduced by about one-half.

In concluson, the questions posed at the beginning of this paper can be answered as follows. The typical form of the genus *Amphipora* has been determined by establishing a neotype that is demonstrated to be representative of the original lost type. The small sponge exhibited various configurations of skeletal features as it grew, but these can not be arranged in a growth series. Some of these features have been recognized as of generic rank and most have been recognized as of specific rank. The type specimens of amphiporids cannot be an assemblage of individuals but should be a single stem. The organism can be reconstructed as a small sponge growing in large numbers in shallow marine water.

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